The Infra-cerebral Organs of Peripatus.

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With 4 Text-figures.

Attached to the ventral surface of the supra-oesophageal ganglion of Peripatus and hanging therefrom are two small vesicles. They were discovered as far back as 1853 before Peripatus was regarded as an Arthropod, and Grube, their discoverer, considered them to be auditory organs (**8**).

In 1883, Balfour, in his classical description of the anatomy of Peripatus capensis (**2**), described the structure of these vesicles, and after a statement detailing their shape and position added that each consisted mainly of ganglion cells. He continued with the following words: 'In its interior is a cavity with a distinct bounding membrane. . . . At its free end is placed a highly refractive, somewhat oval body, probably forming what Grube describes as a dark spot, half embedded in its substance, and kept in place by the sheath of nervous matter surrounding it. It is difficult to offer any interpretation of the nature of this body. It is removed considerably from the surface of the animal, and is not, therefore, so far as I can see, adapted to serve as an organ of hearing.'

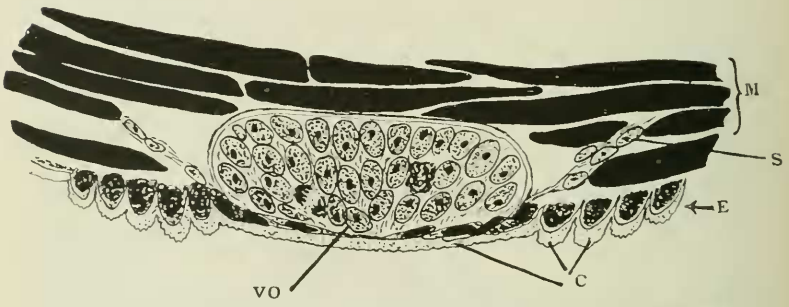
Three years after the appearance of Balfour's paper, Kennel (**11**) followed the development of the infra-cerebral vesicles and discovered that they were apparently homologous with certain groups of cells situated between the legs—and known as the 'ventral organs' (see Text-fig. 1).

This was confirmed by Sedgwick (**15**) in 1888, and the

discovery has very considerably modified the views of the function and meaning of the infra-cerebral vesicles.

If any definite theory of the function of these structures can be said to be generally accepted, it is that they represent the ectoderm from which the nervous system arose in the embryo, and in a recent paper by Duboscq the suggestion is made that the infra-cerebral vesicles remain, even in the adult stage, structures for the renovation or increase in size of the supra-oesophageal ganglia. Cells are supposed to be cut off from the vesicle cells and to migrate into the ganglia, there to become either new nerve-cells or supporting cells.

Text-fig. 1.



Peripatoides occidentalis: section of so-called ventral organ, VO; C, cuticle; E, ectoderm; M, muscles of body-wall; S, strand connecting ventral organ with lateral nerve-cord.

The present note has been written because in several of our best preparations from the head of Peripatoides occidentalis, Dendy, of Western Australia (**5**), the histology of the organs in question is not the same as that illustrated by Duboscq (**6**). And a little more may be said in explanation of the presence of these curiously definite structures.

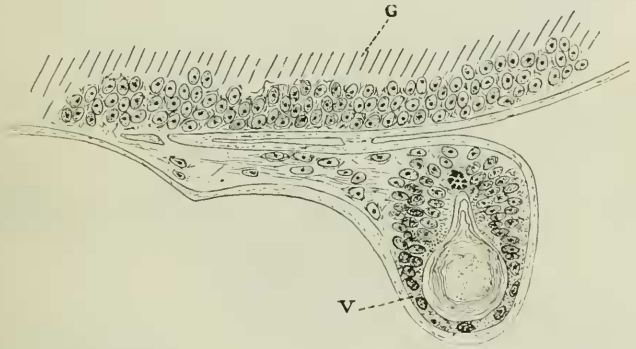
According to Duboscq (who examined Opisthopatus cinctipes, Purcell) one can distinguish in these organs two distinct regions, (*a*) the vesicle, (*b*) the ganglion intermediare. The latter is the part which former writers have called the stalk or peduncle of the vesicle. The term 'ganglion intermediare' is unsuitable, especially since it appears that Duboscq himself

is not sure whether the cells of this part are nerve-cells or merely supporting cells.

There is nothing that might be termed the ganglion intermediare in Peripatoides occidentalis (Text-figs. 2 and 3).

The vesicle is described by Dubosc q as containing nothing within the cavity but serous fluid, there being no refringent oval body of the kind referred to by Balfour. (Unfortunately Balfour's figure gives no idea of the histology of the infra-cerebral vesicles.) Now we have found occasionally that

TEXT-FIG. 2.



Infra-cerebral vesicle, with enclosure, from adult Peripatoides occidentalis. ×530. G, ganglion; V, infra-cerebral vesicle.

bodies do occur within the cavity, reminding one of Balfour's description, and the Text-fig. 2 is from the best preparation of this character. It is part of a transverse section through the head. The structure is referred to below.

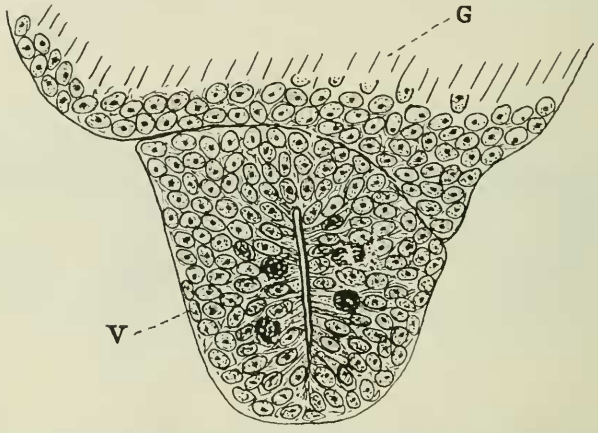
The infra-cerebral organs appear in dissections to hang from the supra-oesophageal ganglion by short stalks. In sections, however, they appear more closely attached. The difference in appearance is due to the transparency of the suspending membrane which is the structureless, almost non-staining, sheath of the ganglion. In Peripatoides occidentalis there is generally a region that one might term the peduncle, within which are a few scattered nuclei and a small number

of delicate fibre-like strands. They might be nerve-fibres or, on the other hand, merely processes of non-nervous cells.

In young and small Peripatoides (Text-fig. 3) the conditions are somewhat different, however, and the walls of the vesicles are not so distinctly separated from the cerebral ganglia (see Text-figs. 2 and 3).

In the adult the infra-cerebral vesicle is covered by the neurilemma or sheath of the supra-oesophageal ganglion, and

TEXT-FIG. 3.



Infra-cerebral organ from young Peripatoides occidentalis. ×400.

this layer almost cuts it off from the latter. According to Saint-Rémy (**14**) and Duboscq (**6**) the sheath is pierced by numerous pores, through which bipolar cells are to be seen migrating into the brain. This is hardly the case in the adult Peripatoides, as the figure shows. There are only a few fibres passing from the vesicle into the supra-oesophageal ganglion and but a few nuclei occur here and there.

The cells of the vesicle itself are not of the same depth throughout. Ventrally the walls are thin whilst laterally they are thick, and the cells are slender, so that the nuclei lie at different levels. The nuclei resemble closely those of the ganglion cells of the brain mass.

The cavity of the vesicle is most usually empty, but sometimes contents are present, and the most conspicuous example of this kind has been figured (Text-fig. 2). In this specimen there is a non-granular mass surrounded by a number of concentric lamellae—almost like a decalcified concretion. The occasional presence of an enclosed body is very interesting.

TEXT-FIG. 4.

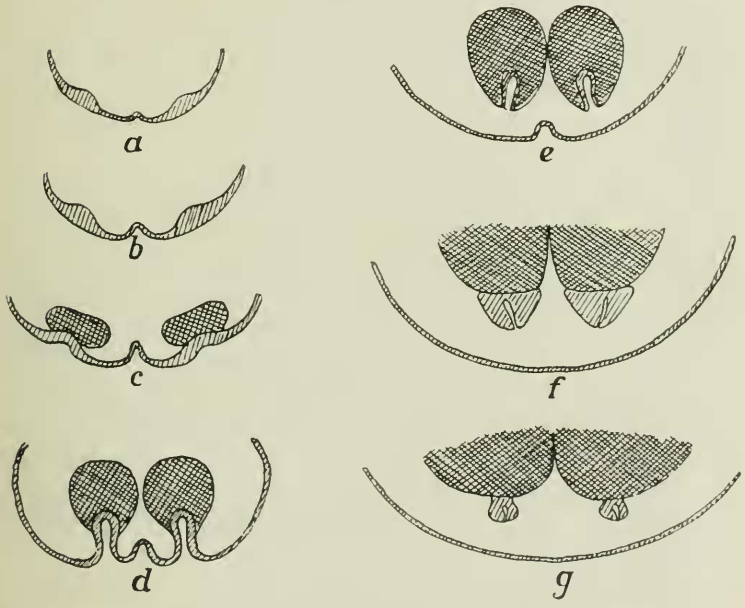


Diagram illustrating development of infra-cerebral vesicles in Peripatus occidentalis.

At first it was thought to be due to fixation, but there is no reason to believe that such is the case. Evidently the vesicle cells may sometimes secrete into the central cavity. Thus a feature recorded by Balfour has again been found and in another species. The few writers who have mentioned the infra-cerebral vesicles since the date of Balfour's paper seem to have doubted its occurrence. No cilia are found within the vesicle nor is there any very definite lining membrane.

The development of these infra-cerebral vesicles is now well known. They arise as invaginations of the ectoderm (Text-fig. 4) which is concerned in the formation of the supra-oesophageal ganglia, and at first they are open to the exterior (to the buccal cavity or near it), so that at this stage the supra-oesophageal ganglia possess cavities which are open below. The cavities become closed and then, whilst increase in size of the ganglia takes place, they remain almost of the original size (a slight decrease takes place if anything), and the surrounding cells, which are indistinguishable from the ganglion cells, become separated and pinched off from the brain mass, until finally two small distinct vesicles lie appended as we have seen. The diagrams illustrate how this takes place.

One other feature of considerable importance remains to be stated. In the adult one may occasionally find cells in the infra-cerebral body undergoing mitotic division. This was first described by Duboscq. We find, however, that the number is much reduced as the animal becomes larger, and they are only occasionally found in the full-sized specimens. In the small Peripatus, not long born, they are more numerous (see Text-fig. 3). It may be stated here that the same feature is to be met with in the so-called ventral organs (Text-fig. 1). This fact has not been recorded before and it completes the resemblance between the ventral organs and the infra-cerebral vesicles. There can be little doubt of their homology.

Discussion.

The infra-cerebral vesicles of Peripatus were once considered to be sense organs concerned in hearing. Probably this was by analogy with the little vesicles often found close to the supra-oesophageal ganglia in the Polychaets and certain other Invertebrata and once termed Otocysts. They are now usually regarded as Statocysts or organs of orientation. Duboscq concludes, however, that in Peripatus they are not sense organs, nor glandular structures, but that in the adult as well as in the embryo they are organs for the production of either nerve-cells or neurogloea cells (supporting cells).

The vesicles known as statocysts or otocysts in the Invertebrates are still of questionable function in many cases. This is particularly so in the case of certain Nemertines (Metanemertines) (**3**), where the walls of the vesicles are surrounded by the ganglion cells of the brain mass and no cilia are present. In fact they are not unlike the infra-cerebral vesicles of Peripatus. On the other hand, in Molluscs such as Pterotrachea, where each statocyst contains a statolith supported on bunches of cilia, the circumstances are altogether different, as experiment has shown. Amongst Polychaet worms statocysts are known in Sabellidae, some Terebellidae, Arenicola, Aricidae, and some Alciopidae. In some cases cilia are found within the vesicles, and statoliths are present (either secreted, or consisting of sand grains from the exterior). In the Arenicola species, however, the state of development of the 'statocysts' varies within very wide limits and it is difficult to express any opinion about the function of these organs. They appear to develop from invaginations of the ectoderm, but there is not the close connexion with the development of the cerebral ganglia which is so characteristic of Peripatus. Are these vesicles homologous?

It is interesting to look at the condition of things amongst the Tracheata.

In none of the Tracheata do the organs of orientation take the form of statocysts associated with the supra-oesophageal ganglion. But in the development of the supra-oesophageal ganglion of the Myriapoda it is certainly very striking that pit-like depressions occur on the ventral surface which afterwards become closed vesicles and later disappear (**10**). The same thing is true of the Insecta and Arachnida (**1** and **12**).

In the Crustacea there is, so far as I am aware, no evidence of pit-like depressions of this kind during development. Statocysts are found, but these are not at all homologous with the organs we are considering and occur in very different situations. Curiously enough, there is a striking exception. Thus, according to Claus (**4**), two otocysts are found connected with the cerebral ganglion in certain Amphipoda—the Platyscelidae. The same author mentions two vesicles as of similar function in the

brain of a Copepod—Eucalanus attenuatus (Dana), but Esterly (**7**) considers these to be optical in function and apparently their structure is quite different from that of the other brain vesicles we have dealt with.

We would suggest, therefore, that the infra-cerebral vesicles of Peripatus are homologous with the cephalic pits of other Tracheate embryos. In these cases the pits become closed off, the walls become parts of the cerebral ganglion, and the cavities disappear altogether. In Peripatus, on the other hand, the vesicles remain, but they are gradually constricted off from the rest of the supra-oesophageal ganglion. The adult condition in Peripatus is, then, an embryonic stage in the Myriapoda. In the adult it is probable that the infra-cerebral vesicles serve no special function—they are not really 'organs' at all—they may still be regarded as parts of the supra-oesophageal ganglion. Possibly their wall contains a few ganglion cells from which fibres pass into the deeper parts of the brain mass. The occasional presence of bodies within the cavity is interesting, but this suggests nothing more than the ectodermal origin of the cells of which the vesicle is composed, and the tendency for the secretion of a chitinous cuticle.

In the earlier stages before growth is complete this portion of the supra-oesophageal ganglion retains some of its former power of growth and continues to give rise to cells by division (as observed by Duboscq), but it is not a special organ for this purpose and loses its function in the adult.

Whether this character, apparently common to the Tracheates, is homologous with the statocysts found occasionally in the worms is another matter—quite impossible as yet to decide. It has been affirmed, however, that in certain Annelids (Lopadorhynchus) the supra-oesophageal ganglia develop in connexion with ciliated pits, which degenerate somewhat afterwards (**13**). This is very suggestive.

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